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RESEARCH ARTICLE

Adapting the growth-form concept to geniculate coralline algae (Corallinales, Rhodophyta)

Jakop Schwoerbel[1,2] | **Juliet Brodie**[3] | **Martha S. Calderon**[4] | **Guillermo Diaz-Pulido**[5] | **Paul W. Gabrielson**[6] | **Aki Kato**[7] | **Line Le Gall**[8] | **Gavin W. Maneveldt**[9] | **Clio Maridakis**[8] | **Patrick T. Martone**[2] | **Isabella Moro**[10] | **Robert J. Mrowicki**[3] | **Wendy A. Nelson**[11] | **Viviana Peña**[12] | **Fabio Rindi**[13] | **Florence Rousseau**[8] | **Tom Schils**[14] | **Frederico T. S. Tâmega**[15] | **Riccardo Trentin**[10]

[1]Australian National Algae Culture Collection, CSIRO, Hobart, Tasmania, Australia

[2]Department of Botany and Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia, Canada

[3]Natural History Museum, Research, London, UK

[4]Instituto de Investigación de Ingeniería Ambiental (INAM), Facultad de Ingeniería Ambiental, Biosistema y de la Energía (FIABE), Universidad Nacional Toribio Rodríguez de Mendoza de Amazonas (UNTRM), Chachapoyas, Amazonas, Peru

[5]School of Environment and Science, Griffith University, Nathan, Queensland, Australia

[6]Biology Department and Herbarium, University of North Carolina at Chapel Hill, Chapel Hill, North Carolina, USA

[7]Fisheries Laboratory, Blue Innovation Division, Seto Inland Sea Carbon-Neutral Research Center, Hiroshima University, Takehara, Hiroshima, Japan

[8]Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum National d'Histoire Naturelle, CNRS, Sorbonne Université, EPHE, Paris, France

[9]Department of Biodiversity and Conservation Biology, University of the Western Cape, Bellville, South Africa

[10]Department of Biology, University of Padova, Padova, Italy

[11]Herbarium, Natural Sciences Department, Tāmaki Paenga Hira Auckland Museum, Auckland Domain, Auckland, New Zealand

[12]Grupo de Investigación BioCost, Facultade de Ciencias & CICA – Centro Interdisciplinary de Química e Bioloxía, Universidad da Coruña, A Coruña, Spain

[13]Dipartimento di Scienze della Vita e dell'Ambiente, Università Politecnica delle Marche, Ancona, Italy

[14]Marine Laboratory, University of Guam, Mangilao, Guam

[15]Departamento de Biotecnologia Marinha, Instituto de Estudos do Mar Almirante Paulo Moreira, Arraial do Cabo, Rio de Janeiro, Brazil

Correspondence
Jakop Schwoerbel, Australian National Algae Culture Collection, CSIRO, 3-4 Castray Esplanade, Hobart 7004, Tas., Australia.
Email: jakop.schwoerbel@botany.ubc.ca

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Abstract

Geniculate coralline algae (Corallinales, Rhodophyta) are a diverse group of calcifying macroalgae, loosely united by flexible upright axes formed by alternating calcified (intergenicula) and uncalcified segments (genicula), a trait that has independently arisen several times. To standardize terminology, the concept of growth forms (i.e., the external gross morphology of a specimen) was developed previously for non-geniculate (without joints) corallines, but no such efforts have been undertaken for geniculate corallines. Here, we adapted the growth--form concept to geniculate corallines. We propose that, based on their branching pattern and two- or three-dimensional branch arrangement, geniculate corallines can be grouped into seven growth forms: *unbranched* (unbranched uprights), *feather-like* (complanate, pinnate branching), *fan-like* (complanate, dichotomous branching), *irregular* (complanate or multiplanar without a clear branching pattern), *whorled* (multiplanar, verticillate

branching), *arbuscular* (multiplanar, dichotomous branching), and *plumose* (multiplanar, pinnate branching). We have provided a dichotomous key to assign specimens to different growth forms and discussed examples of each of these growth forms as well as the concept of intergrades between them. Additionally, we have provided a glossary of terms used in the growthform definitions and for intergenicular morphology. These tools will be a helpful resource for ecologists, taxonomists, beachcombers, and anyone interested in these comparatively little-studied but diverse macroalgae.

KEYWORDS
articulated coralline algae, branching pattern, growth habit, intergenicular morphology

INTRODUCTION

Coralline algae (orders Corallinales, Corallinapetrales, Hapalidiales, and Sporolithales in the subclass Corallinophycidae) are a diverse group of almost exclusively marine, calcifying, red algae observed throughout the photic and mesophotic zones in near-shore habitats (Johansen, 1981; Schubert et al., 2020; Sissini et al., 2022; Tâmega et al., 2021; Žuljević et al., 2016). They are characterized by the deposition of high magnesium calcite in their cell walls (Cabioch & Giraud, 1986; Nash et al., 2019) and have important ecological roles, building biogenic habitats (Bosence, 1983a; Rindi et al., 2019), stabilizing reefs (Barnes & Chalker, 1990), and promoting larval and algal settlements (Abdul Wahab et al., 2023; Spotorno-Oliveira et al., 2015; Twist et al., 2024). Based on external morphology, coralline algae have traditionally been separated into two groups that have otherwise no phylogenetic basis (Cabioch, 1971; Hind et al., 2018; Johansen, 1981): non-geniculate or non-articulated corallines (entirely calcified, without uncalcified joints) and geniculate or articulated corallines (with uncalcified joints). Geniculate corallines are characterized by upright flexible axes, which generally arise from a crustose, non-geniculate base or a small discoid holdfast. Their flexibility is the result of uncalcified joints (genicula) that alternate with calcified segments (intergenicula), usually longer than the genicula (Janot & Martone, 2016, 2018; Martone & Denny, 2008). Geniculate corallines have evolved from non-geniculate ancestors at least three times (Janot & Martone, 2018; Johansen, 1981), but only in the Corallinales, specifically the families Corallinaceae, Lithophyllaceae, and Porolithaceae, and are absent in the Sporolithales, Corallinapetrales, and Hapalidiales (Peña et al., 2020). In addition, recent work demonstrated that some non-geniculate corallines evolved from geniculate ancestors, reflecting evolutionary reversals (Hind et al., 2016, 2018; Johansen, 1974; Martone et al., 2012; Peña et al., 2020). In some cases, diminutive geniculate fronds represent a reduction in morphological complexity, not an evolutionary intermediate between non-geniculate and geniculate morphologies (Martone et al., 2012).

Coralline algae have had a long and turbulent taxonomic history (see Johansen, 1981 and Leão et al., 2024 for more detailed accounts). First considered plants, then animals similar to corals, corallines were firmly recognized as red algae by Philippi (1837) based on their internal structures. Initial generic and species descriptions of geniculate corallines focused on branching patterns (Lamouroux, 1812, 1816), which were subsequently augmented by the use of smaller scale morphological characters, including the type of reproductive structures (Decaisne, 1842), and anatomical characters, such as the internal structures of intergenicula (van Weber Bosse, 1904; Yendo, 1905) or cell connections (Cabioch, 1971; Johansen, 1981). Current taxonomy for geniculate corallines is increasingly based on the use of DNA sequence data, which has revolutionized coralline algal systematics and species discovery in recent decades (Calderon et al., 2021; Gabrielson et al., 2011; Martone et al., 2012; Nelson et al., 2025; Pardo et al., 2015; Schipper et al., 2023; Twist et al., 2020; Wade et al., 2023).

To standardize the terminology for species descriptions of non-geniculate corallines, Woelkerling et al. (1993) published a synopsis of growth forms (the external appearance of specimens) based on several older systems (Bosence, 1976, 1983b; Johansen, 1981), which was recently further revised (Maneveldt et al., 2026). Growth forms were based on and applied to individual specimens, which made them independent of taxonomic groups, and any one growth form can apply to specimens from many different lineages (Woelkerling, 1988). Individuals can also display intergrading growth forms (defined as having a growth form that cannot be placed into either of two discrete growth forms), and species may exhibit a variety of growth forms across individuals (Hernandez-Kantun et al., 2015). Given this often high degree of morphological variability within and

between specimens, growth forms provide a standardized tool for descriptions that are independent of taxonomy.

Growth forms of geniculate corallines are sometimes mentioned in the literature, but to date, no standardized or commonly used terminology exists (Farr et al., 2009; Harvey et al., 2020). Johansen (1981) loosely described several growth forms based on a mixture of branching patterns, intergenicular morphology, and conceptacle position, as well as branch "quality" (delicate vs. robust). However, the use of qualitative characters and the lack of names for these growth forms has resulted in difficulty with interpretation and inconsistent application. Unlike early descriptions of non-geniculate corallines, descriptions of geniculate corallines, in general, have suffered less from ambiguous terminology when describing growth forms, mostly because the botanical terminology used for branching patterns is well established and leaves little room for misinterpretation (Stearn, 1992). However, where existing terminology falls short is in describing the overall growth habit of geniculate individuals in a concise fashion as well as that variation within and between specimens of the same species. Such information is particularly relevant to specialists looking to describe the morphological range of species and to non-specialists confronted with the challenges of coralline taxonomy. Well-defined growth forms also can provide insight into the biology and ecology of species and any associated flora and fauna but, more importantly, provide a consistent reference for interpretations of external morphologies (Littler et al., 1995; Littler & Littler, 1999, 2000, 2003, 2013; Maneveldt et al., 2026; Maneveldt & Keats, 2014; Rivera et al., 2004).

The challenge in applying the growth-form approach to geniculate corallines lies mainly in the number of external characters that define their overall shape. In non-geniculate corallines, the growth form is largely based on the external appearance, which yields several clear main groups, each with several subdivisions (Maneveldt et al., 2026; Woelkerling et al., 1993). Broadly speaking, most geniculate corallines would fall into the *arborescent* growth form (upright with distinct holdfast), not including unattached specimens, called articuliths (Tâmega et al., 2021; Taylor & Saunders, 2025). However, the arborescent shape can be the product of a variety of branching patterns, which combine with other macroscopic features such as intergenicula shape or holdfast morphology. Quick assessment of geniculate corallines in the field is further complicated by the flexibility of the fronds, which can obscure characters such as the branching plane, compared to the mostly inflexible, solid forms of non-geniculate corallines. The issue remains, therefore, to find a sufficiently detailed system that is broadly usable without requiring high levels of specialist knowledge.

Like Woelkerling et al. (1993) for non-geniculate corallines, we have defined growth form for geniculate corallines as the external appearance of a specimen, but unlike Johansen (1981), we have focused mostly on branching patterns and two/three-dimensionality as the basis for the shape of a specimen. Geniculate corallines can have consistently varying branching patterns in different branch orders, defined as the subsequent levels of branching observed in a branched frond, that is, primary, secondary, etc. (Lugilde et al., 2017). The external appearance of a specimen will, therefore, be significantly influenced by the branching pattern of the dominant branches; it can, therefore, be difficult to separate the branching pattern in geniculate corallines from the gross external morphology.

The terminology used for the geniculate coralline growth forms is summarized in Table 1. Terminology surrounding intergenicular morphology is summarized in Table 2 and examples are shown in Figure 1. Crucially, the growth forms are not meant to be a replacement for a detailed description of important taxonomic characters but instead to provide an easily interpretable way to convey the two- and/or three-dimensional structure of an individual specimen, which is otherwise often lost during the collection and preservation process. Although the growth forms do not necessarily reflect phylogeny or taxonomic identification, they may still help to identify species at a local level or genera with very distinct species, such as *Metagoniolithon* spp. (Ducker, 1979) or *Chiharaea* spp. (Martone et al., 2012). Additionally, the growth forms provide a method to increase the resolution of survey data by grouping corallines by growth form in cases where species-level identification is not feasible.

In the following account, we have proposed seven growth forms for geniculate corallines and a dichotomous key for their identification. Specific names for these growth forms are given in **bold** in headings as well as in *italics* throughout the text. We do not differentiate between branch orders for the growth forms. In cases of extreme differences in branching pattern from one branch order to the next, specimens can be assigned to growth-form intergrades, a common occurrence for geniculate corallines (see Discussion). When we refer to individual specimens, we have provided the herbarium accession number where possible, with abbreviations following Index Herbariorum (Thiers, 2026), and references to illustrations of the specimen(s) in the literature. All species names for material that have not been verified by DNA sequencing of type specimens are given in quotes (e.g., *Jania "rosea"*).

TABLE 1 Alphabetical glossary of terms relating to geniculate coralline growth forms.

Bipinnate	Pinnate main axis with pinnate secondary branches
Branchlet	Secondary branch cluster. Can include further branching (tertiary, etc.)
Branch order	Subsequent levels of branching observed in a branched frond. Also see primary/secondary branching
Complanate	Arranged in a single plane
Corymbose/iform	Type of branching where the terminal parts of the branches end at the same height creating a flat or only slightly rounded top
Crustose base	Holdfast consisting of a calcified crust. Resembling encrusting non-geniculate corallines, but giving rise to at least one, usually many uprights (Figure 1s)
Crust	See crustose base
Decussate	Branches opposite to each other. Each branch pair is orthogonal to the one below and the one above
Dichotomous	Branching in two approximately equally thick branches by division at the apex without a percurrent axis Pseudodichotomous branching refers to a split in unequal parts
Distichous	Complanate branching. Can be alternate and opposite
Furcate	Dividing into two, but not at the apex
Frond	One upright axis. Individuals with crustose bases often have multiple fronds arising from the same base
Irregular	Lacking a consistent branching pattern
Palmate	Resembling a hand with spread fingers
Percurrent axis	Main axis of growth extending in a line from the holdfast to the tip of the uprights of an individual
Pinnate	Branching either side of a percurrent axis, giving the appearance of a feather. Can be alternate-distichous or opposite-distichous. Derived from the Latin *pinna*, meaning feather
Polychotomous	Dividing into more than three, without a percurrent axis
Primary branching	Branches originating from the main axis. Synonymous with first-order branching
Secondary branching	Branches originating from primary branches. Synonymous with second-order branching
Stolon	Creeping axis terminating in small discoid holdfasts anchoring the coralline to a substrate (Figure 1q,r)
Stoloniferous	Bearing stolons
Trichotomous	Dividing into three, approximately equally thick branches
Verticillate	Arranged in whorls around a single point of origin (e.g., one geniculum)

Note: Most of these terms are related to the type of branching (primary and secondary). For a more comprehensive glossary on terminology related to coralline algae, see Johansen (1981). See Table 2 for terms relating specifically to intergenicula morphology.

GROWTH FORM DEFINITIONS

Unbranched (Figure 2)

Upright axes unbranched, each with a basal geniculum and additional genicula if comprised of more than one intergeniculum. Often arising from an extensive crustose base. Upright axes are sparse to crowded. Intergenicula terete to compressed.

Feather-like (Figure 3)

Individuals with pinnate (feathered), complanate branches. Clear percurrent (continuous central) axis with either alternate or opposite branches on either side (i.e., alternate-distichous or opposite-distichous). Branch frequency can vary from sparse (several intergenicula between branches, Figure 3b) to dense (branching at every intergeniculum,

TABLE 2 Alphabetical glossary for terms concerning intergenicula morphology.

Awl-shaped	See subulate (Figure 1k)
Barrel-shaped	Terete and tapering toward both ends, shaped like a barrel (Figure 1b). Also see spindle-shaped
Clavate	Terete and wider at the apex than at the base, club-shaped (Figure 1l)
Club-shaped	See clavate
Compressed	Flattened in cross-section
Cornicula	Horn-like appendages arising from the distal ends of conceptacles or intergenicula (Figure 1p)
Cuneate	Wedge-shaped, approximately triangular, and compressed (Figure 1d). Longer than wide. See obcuneate for the inverse
Globular	Terminating in a sphere (Figure 1n), usually referring to apical intergenicula or conceptacles
Fan-shaped	See flabellate
Flabellate	Terete to compressed with distal ends compressed and broadened into a fan shape (Figure 1j). Distal edge can have an irregular outline
Fusiform	See spindle-shaped
Hexagonal	Six-sided (Figure 1c). Sometimes used interchangeably with cuneate
Lobed	With lateral extensions expanding beyond the distal end of the intergeniculum (Figure 1f,g). See winged for comparison
Obovate	Wider at the apex than at the base (Figure 1m). See ovate for the inverse
Obcuneate	Inversely wedge-shaped, with the greatest width near the base. See also cuneate for the inverse
Ovate	Wider at the base than at the apex without sharp corners, terete. Egg-shaped. See obovate for the inverse
Paddle-shaped	Terete to compressed with distal ends flattened and broadened (Figure 1i)
Parallel-sided	The two longest sides lie parallel (e.g. Figure 1a). See trapeziform for comparison
Pear-shaped	See pyriform
Pyriform	Pear-shaped (Figure 1o); usually referring to apical intergenicula or conceptacles
Sagittate	Compressed, with all distal corners tapering to sharp (acute) points and extending beyond the upper edge (Figure 1e). Shaped like an arrowhead. From Latin *sagitta*, meaning arrow
Spindle-shaped	Terete and tapering strongly toward each end. See also barrel-shaped
Subterete	Cylindrical, but slightly compressed. See terete
Subulate	Awl-shaped, tapering to a distal point (Figure 1k)
Terete	Cylindrical
Terminal	Without bearing further branches
Trapeziform/ trapezoidal	Having at least two parallel sides, shaped like a trapezoid (e.g., Figure 1a,b,g)
Truncate	Appearing cut off
Ungulate	Hoof-shaped. Usually referring to apical intergenicula or conceptacles. See Cordero and Paciente (1977) for a schematic drawing of ungulate terminal intergenicula in *Jania ungulata*
Wedge-shaped	See cuneate
Winged	With flattened extensions to either side, resembling wings (Figure 1h). See lobed for comparison

Note: Distal and proximal in the descriptions are in relation to the holdfast or crustose base. See Figure 1 for a visual glossary.

Figure 3f). Intergenicula shape also affects the appearance of dense or coarse branching, with long and thin intergenicula often giving a coarse appearance (Figure 3d). Individuals can be wholly or partially bipinnate (Figure 3d). Primary branches are occasionally dichotomous (regularly dividing into two distinct branches). Individuals are generally attached but might also occur free-living (as articuliths). Upright axes arising from sometimes extensive crusts in attached specimens (Figure 3e). Otherwise, rhizoidal (root-like) holdfasts with or without stolons (creeping horizontal structures that can attach to the substrate and produce new uprights). Known intergrades exist between *feather-like*, *fan-like*, *irregular*, and *plumose*.

Fan-like (Figure 4)

Individuals with dichotomous (regularly dividing into two distinct branches) or furcate (forking) branches (occasionally polychotomous or irregular), all or mostly complanate. No percurrent (continuous central) axis evident. Individuals are attached with small rhizoidal

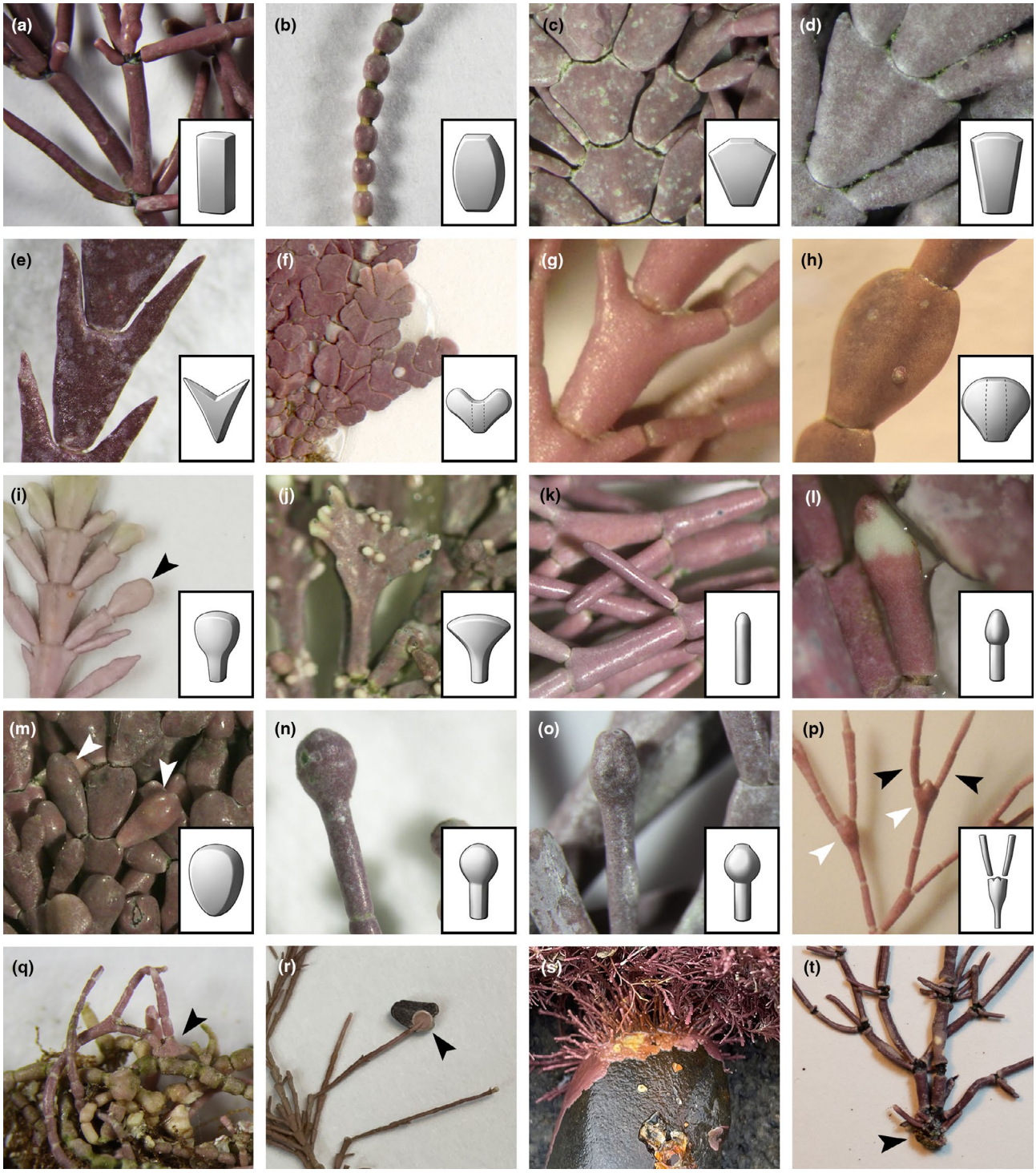

FIGURE 1 A selection of common intergenicular shapes, including terminal conceptacles (l–p). (a) Trapeziform/trapezoidal. (b) Barrel-shaped. (c) Hexagonal; note the clearly defined short edges. (d) Cuneate/wedge-shaped. (e) Sagittate. (f) Lobed. (g) Trapeziform with distal lobes. (h) Winged. (i) Paddle-shaped (arrow). (j) Flabellate/Fan-shaped with irregular terminal edge. (k) Subulate/awl-shaped terminal intergenicula. (l) Clavate/club-shaped. (m) Obovate (arrows). (n) Globular. (o) Pyriform/pear-shaped. (p) Conceptacles (white arrows) with cornicula (horns; black arrows). (q) Stolons with small discoid base (arrow). (r) Stolons terminating in a discoid holdfast (arrow). (s) Crustose base of *Corallina* '*berteroi*' with many uprights. (t) Discoid holdfast (arrow). Images: (a–e, h–o, q, r, t) Jakop Schwoerbel; (g, p) Viviana Peña; (f, s) Patrick Martone.

(root-like) or encrusting holdfasts, sometimes with stolons (creeping horizontal structures that can attach to the substrate and produce new uprights), but might also occur free-living (without attachment). Known intergrades exist between *feather-like*, *fan-like*, *whorled*, *irregular*, and *arbuscular*.

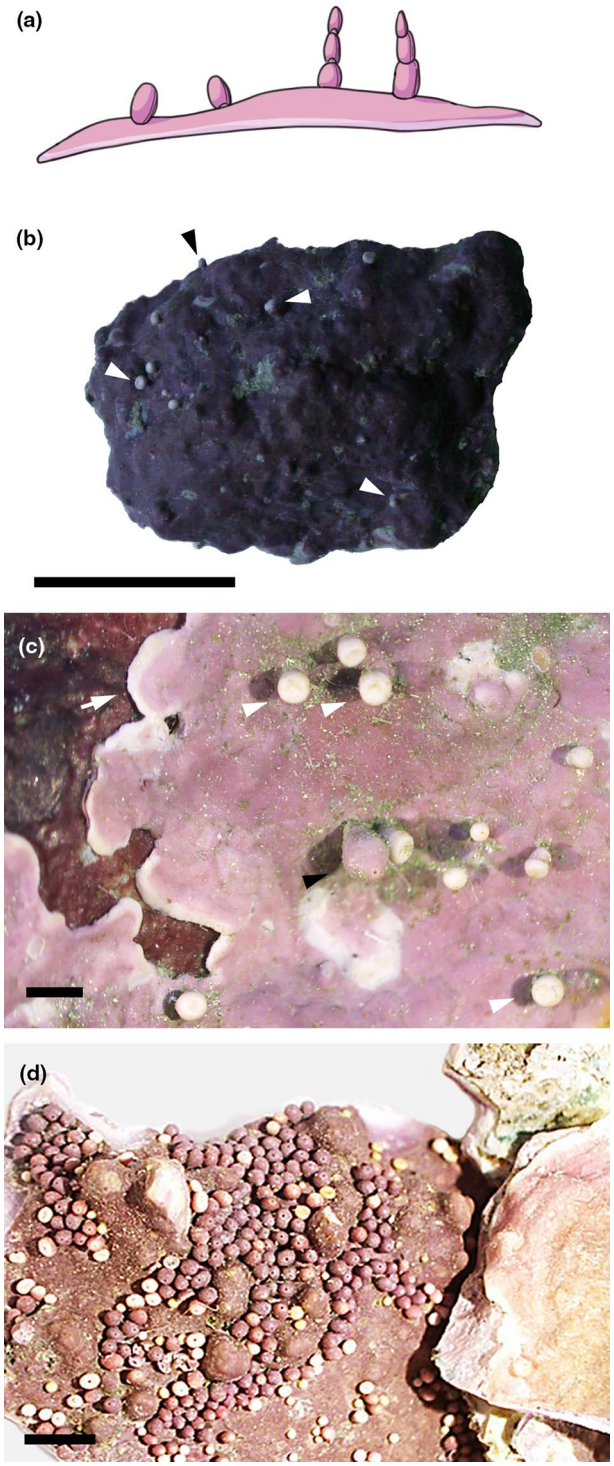

FIGURE 2 Examples of the *unbranched* growth form. All scale bars = 1 cm. (a) Schematic drawing of the growth form. (b) *Chiharaea americana* (PTM1198). Arrows indicate intergenicula. McMullen Island, NE, Canada. (c) *Chiharaea americana* (UBC A062465 as *Yamadaia americana*) with single intergeniculum uprights (arrowheads). Fertile intergeniculum with conceptacle visible (black arrowhead). Numerous intergenicula with eroded conceptacles (white arrowheads). Note the extensive crust (edge at the white arrow). Haddington Island, British Columbia, Canada. (d) *Corallina berteroi* (Chiba, Japan, UBC A62034). Images: (b) Patrick Martone; (c) Paul Gabrielson; (d) Paul Gabrielson, adapted from Calderon et al. (2021, figure 3).

Irregular (Figure 5)

Individuals without a consistent branching pattern, but that may be in part dichotomous (regularly dividing into two distinct branches), with inconsistent branch angles (Figure 5d), distichous (a clear central axis with alternating or opposite side branches, Figure 5b–d), or decussate (orthogonally stacked side branches) in different parts of the individual. Specimens are generally three-dimensional but can sometimes appear two-dimensional depending on the branch arrangement. Such irregular branching may be due to mechanical damage to fronds from herbivory or environmental conditions, leading to individuals with abnormal appearance. Attached or free-living (articuliths). *Irregular* intergrades with all other growth forms except the *unbranched* growth form.

Whorled (Figure 6)

Individuals whorled/verticillate (with branches arising radially from the genicula). Individuals attached by a discoid (disc-like) holdfast. Primary branching often dichotomous (regularly dividing into two distinct branches), but meristematic genicula can continue branching, creating false whorls (Ducker, 1979). Intergenicula usually terete (cylindrical). Known intergrades exist between *whorled*, *fan-like*, *irregular*, and *arbuscular*.

Arbuscular (Figure 7)

Individuals with overlapping, dichotomous (regularly dividing into two distinct branches) or furcate (forking) multiplanar secondary branching, resulting in a three-dimensional shape of a small tree (Latin *arbuscula* = small tree). Individual branchlets often *fan-like*. Individuals are attached with small rhizoidal (root-like) or encrusting holdfasts, sometimes with stoloniferous branches (bearing horizontal runners). Branching most commonly at the distal ends (tips) of intergenicula (Figure 7b,c), but occasionally also from the sides of the intergenicula (Figure 7f; Harvey et al., 2020). Three-dimensional shape due to either dense overlapping secondary branches (Figure 7b,d) or multiplanar secondary branches (Figure 7f,g). Attached or free-living. Intergrades exist between *arbuscular*, *fan-like*, *whorled*, and *irregular* growth forms.

Plumose (Figure 8)

Individuals with many *feather-like* branches in a multiplanar arrangement. Overall appearance very three-dimensional due to either dense overlapping complanate branchlets (Figure 8f), bipinnate branching (Figure 8b,d), or multiplanar branching (Figure 8b,d). Primary branching

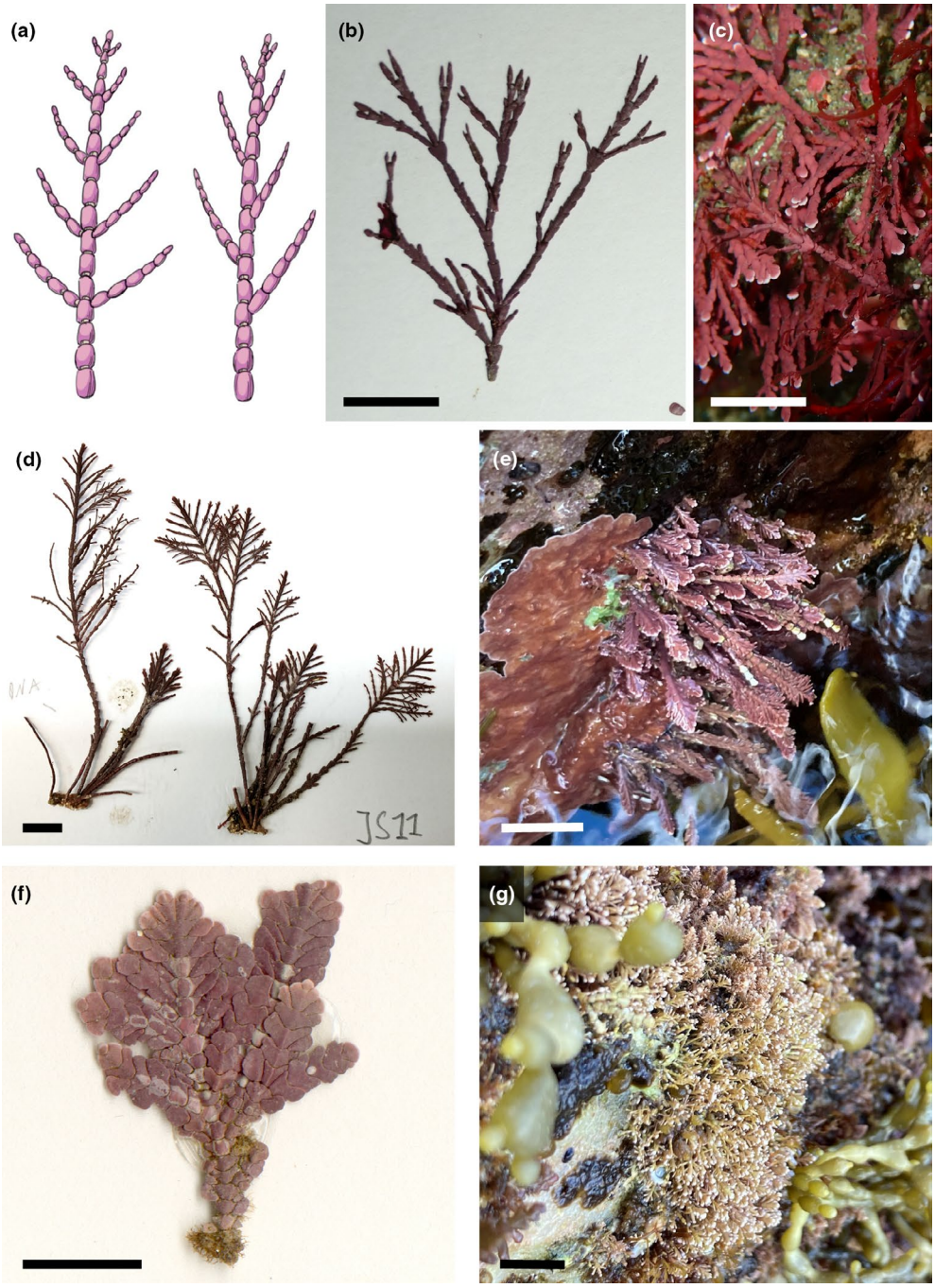

FIGURE 3 Examples of the *feather-like* growth form. All scale bars = 1 cm. (a) Schematic drawing of the growth form with opposite- (left) or alternate-distichous (right) branching. (b) *Arthrocardia* sp. (JS70) with coarse pinnate (feathered) branching. Sisters Bay, Tasmania, Australia. (c) The same specimen in the field. (d) *Corallina* sp. (JS11) with frequent branching but thin terete intergenicula giving the specimen a coarse appearance. Sisters Bay, Tasmania, Australia. (e) *Corallina* sp. with many *feather-like* fronds arising from a large crustose base. Lighthouse Beach, Tasmania, Australia. (f) *Bossiella 'chiloensis'* (UBC A89685) with branching at every intergeniculum and broad lobed intergenicula. Hakai Beach, British Columbia, Canada. (g) Dense batch of *feather-like Corallina 'berteroi'* arising from extensive crusts. Lighthouse Beach, Tasmania, Australia. Images: (b, d, e, g) Jakop Schwoerbel; (c) Matt Rose; (f) Patrick Martone.

often dichotomous (regularly dividing into two distinct branches), especially near the holdfast. Individuals are attached, sometimes arising from extensive crusts, but might also occur free-living. Otherwise, rhizoidal (root-like) or discoid (disc-like) holdfast with or without stolons (horizontal runners). Known intergrades exist between *plumose*, *feather-like*, and *irregular* growth forms.

Dichotomous key to the geniculate coralline growth forms

How to use this key: Branching patterns should be assessed based on the dominant, overall, primary pattern. This makes it possible to disregard small inconsistencies in branching pattern arising from

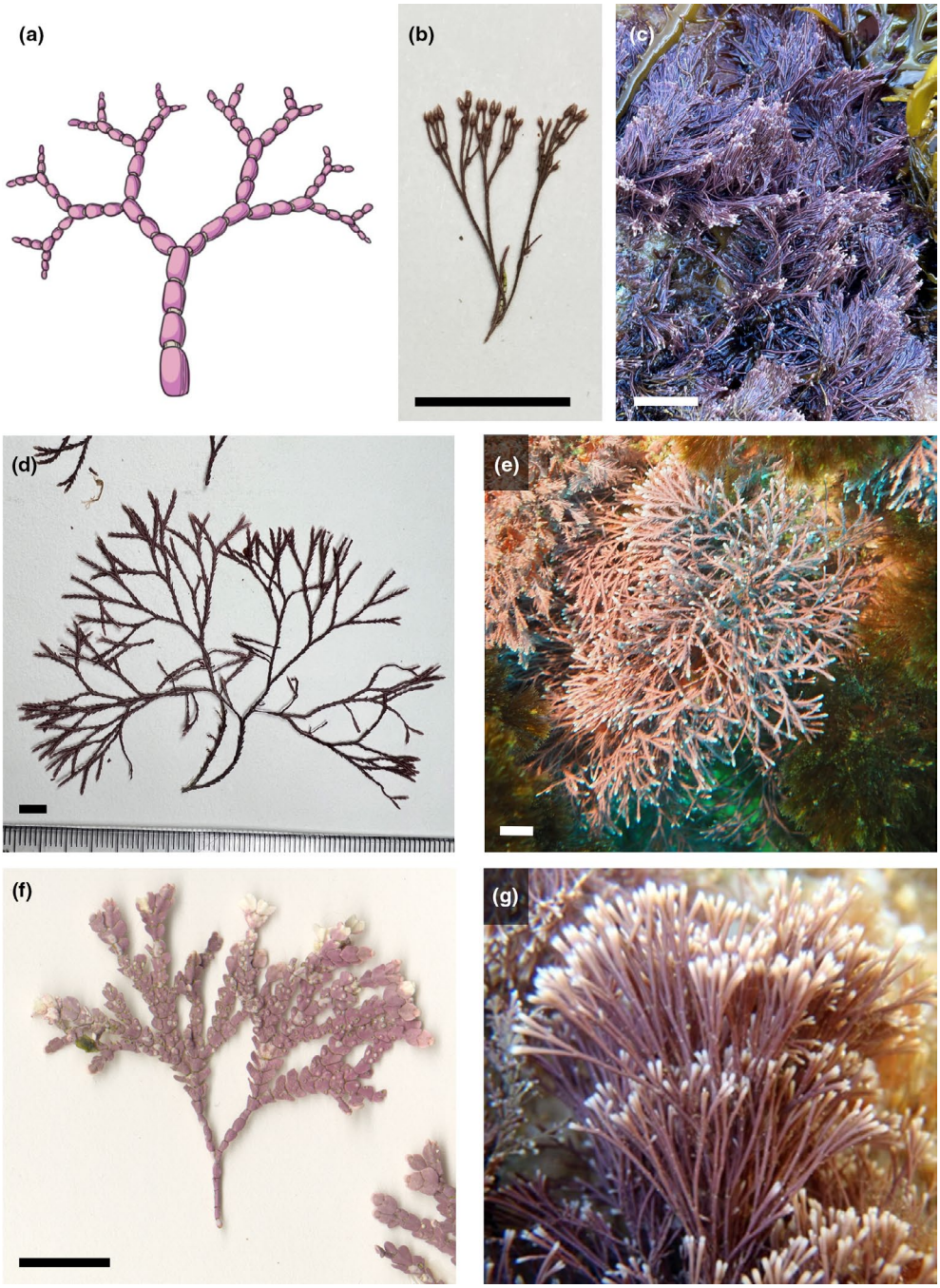

FIGURE 4 Examples of the *fan-like* growth form. All scale bars = 1 cm. (a) Schematic drawings of the growth form with dichotomous branching. (b) *Jania* sp. (JS124) Lighthouse Beach, Tasmania, Australia. (c) The same specimen in the field. Note the dense clusters. (d) *Jania sagittata* (PTM2230) with complanate dichotomous branching. Twin Peaks, Tasmania, Australia. (e) A similar specimen in the field at the same location. (f) *Bossiella dichotoma* (UBC A89560), Hakai, West Beach, BC, Canada. (g) *Jania longifurca*, Spain. Images: (b, c) Jakop Schwoerbel; (d, f) Patrick Martone; (e) Hunter Forbes; (g) Viviana Peña.

mechanical damage or early development. Likewise, in the case of specimens with inconsistent branching patterns in different branch orders, follow the key using the dominant branching pattern. Specimens for which there is a regular distribution of different branching patterns can be assigned to growth-form intergrades (see Discussion). To do this, follow the key using the different branching patterns present. The result can then be noted as, for example, a *feather/fan-like* intergrade. These intergrades are common and specimens should be carefully assessed along the entire individual. For articuliths (unattached geniculate corallines) follow the key using branching patterns and ignore references to attachment/holdfast. The result will then be a "growth form" articulith, for example, *arbuscular* articulith.

Key to the geniculate growth forms:

1a.	Upright axes diminutive, each with few genicula (<10, usually fewer than 5) and lacking branches	**Unbranched**
1b.	Upright axes branched	2
2a.	Upright axes branched in one plane (an individual can have several individually complanate upright axes)	3
2b.	Upright axes branched in more than one plane	4
3a.	Branching pinnate (alternate and/or opposite; feathered), with a clear percurrent (continuous central) axis	**Feather-like**
3b.	Branching dichotomous (regularly dividing into two distinct branches), trichotomous (regularly dividing into three distinct branches), furcate (forked) or polychotomous (regularly dividing into more than three distinct branches), without a clear percurrent (continuous central) axis	**Fan-like**
4a.	Branching verticillate (whorled) with only occasional dichotomies (splits into two) near the base of the individual or near branch apices	**Whorled**
4b.	Branching along main axes pinnate (feathered), dichotomous (regularly dividing into two distinct branches), furcate (forked), trichotomous (regularly dividing into two distinct branches) or without clear pattern	5
5a.	Branching without clear pattern	**Irregular**
5b.	Branching with clear pinnate (feathered), dichotomous (regularly dividing into two distinct branches), furcate (forked) or trichotomous (regularly dividing into three distinct branches) pattern	6
6a.	Branching dichotomous (regularly dividing into two distinct branches), furcate (forked) or trichotomous (regularly dividing into three distinct branches). Secondary branching present and in multiple planes or dense and overlapping. Individual branchlets may be complanate	**Arbuscular**
6b.	Branching pinnate (alternate and/or opposite; feathered), secondary branching present and in multiple planes or dense and overlapping. Individual branchlets may be complanate	**Plumose**

DISCUSSION

The system proposed herein, to standardize the terminology for growth forms of geniculate corallines, was adapted from that for non-geniculate corallines described by Woelkerling et al. (1993) and updated by Maneveldt et al. (2026). These proposed growth forms are not intended to replace detailed morphological and anatomical descriptions for taxonomic accounts but are instead meant to provide a practical and standardized system to describe overall growth habits of individual specimens. Many geniculate species can have a range of growth forms, and references to individual specimens should be taken solely as examples of that growth form, not necessarily representative of an entire species.

In an effort to balance the growth form definitions between specificity and general usability we based the definitions primarily on branching pattern. Branching is one of the most obvious features of geniculate corallines, forming the overall foundation for an individual's growth habit and used in early efforts of geniculate coralline classification (Lamouroux, 1812, 1816). Growth forms could be further augmented by holdfast morphology (e.g., crustose, discoid, and stoloniferous; Table 1), the shape of intergenicula (e.g., terete, flattened, lobed, and sagittate; Table 2), and conceptacle morphology (e.g., hemispherical, globular, ovoid, and urn-shaped pyriform; Table 2). However, although these characters are important for taxonomic delimitation, they may be absent or difficult to assess, thus reducing their general usability. Holdfast morphology depends on the collection of the entire specimen, including its basal attachment, which is often difficult and therefore neglected, especially in subtidal environments and for geniculate corallines with firmly attached, crustose bases. When possible, we urge collectors to make sure that holdfasts are part of collections (insofar as rules in local permits allow), so their usefulness both for the general growth forms and as a taxonomic character can be assessed. Intergenicular shape (e.g., terete, cuneate, hexagonal etc.; Table 2), size, and length/width ratios vary in nearly all geniculate coralline individuals from their base to their apices and thus are complex to report for individuals and species. Conceptacle morphology requires reproductive specimens, limiting its utility to only a subset of specimens. Considering all these potential difficulties, we have only included very broad descriptions of intergenicular and holdfast morphologies in the growth form assessment and excluded conceptacle morphology entirely. In general, we encourage collectors to accompany their specimens with in situ images. This is especially useful in cases where whole specimens (i.e., including the holdfast) cannot be collected.

From a growth-form perspective, geniculate corallines can be grouped into two broad categories: unbranched and branched. The branched category can further be subdivided by branching type (dichotomous, pinnate/feathered, verticillate/whorled, and irregular) as well as overall growth habit (two- or three-dimensional), resulting in a total of seven growth forms: *unbranched*, *fan-like*, *feather-like*, *irregular*, *whorled*, *arbuscular*, and *plumose*.

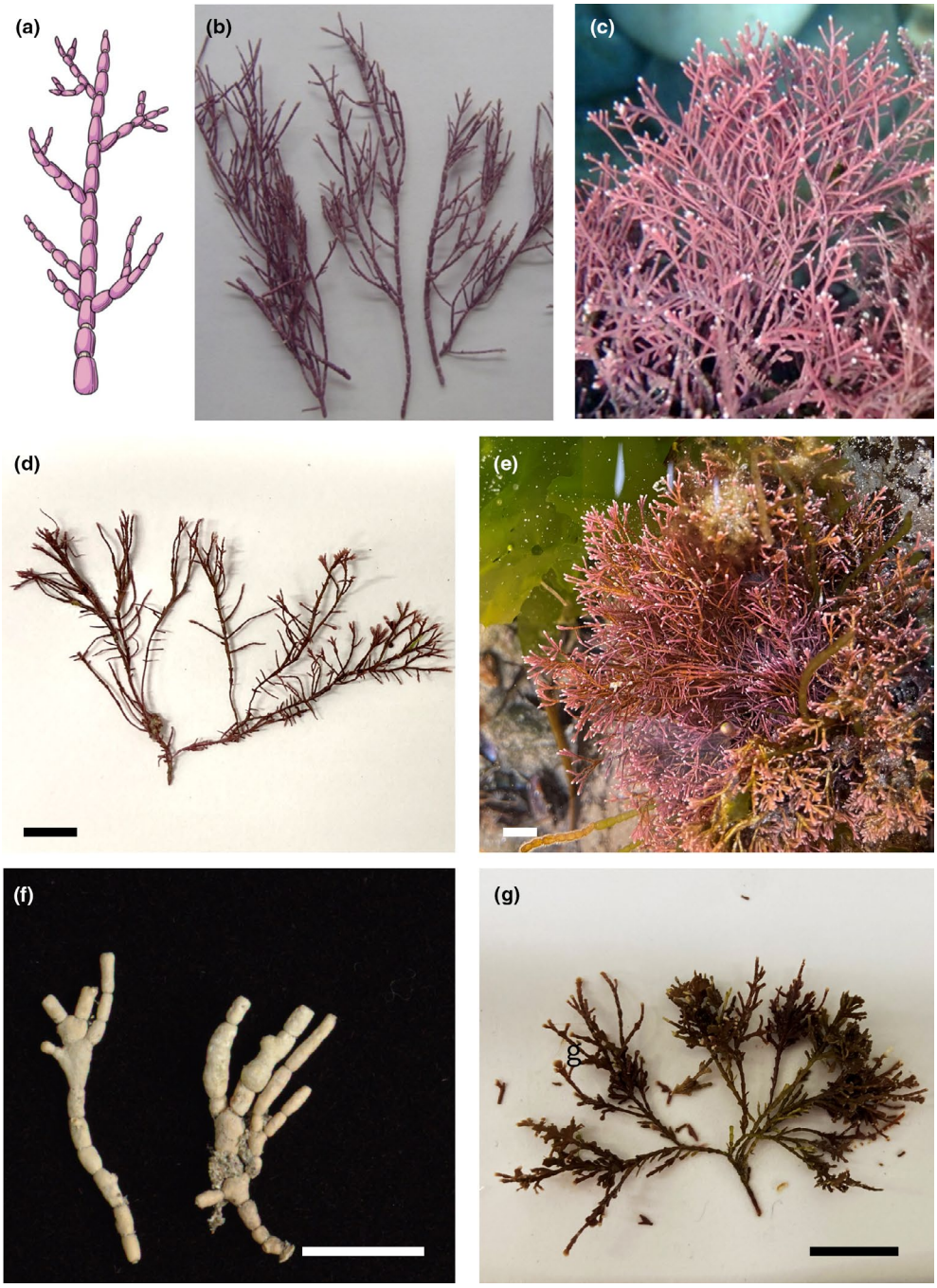

FIGURE 5 Examples of the *irregular* growth form. All scale bars = 1 cm. (a) Schematic drawing of the growth form. (b) *Corallina officinalis* (SANT-Algae 27687). A Coruña, Galicia, Spain. (c) A similar specimen in the field. (d) *Jania 'longifurca'* (PTM2198) showing a mix of branching patterns. Tessellated Pavement, Tasmania, Australia. (e) The same specimen in the field. (f) *Corallina officinalis* (S A2012) with the *irregular* northeast Pacific morphotype, initially described as *Pachyarthron cretaceum*. Bering Island, Bering Sea, Russia. (g) *Corallina berteroi* (JS116), Blackmans Bay, Tasmania, Australia. Images: (b, c) Vivina Peña; (d, e) Patrick Martone; (f) Paul Gabrielson; (g) Jakop Schwoerbel.

Articuliths are a notable omission from our proposed growth forms. They are unattached, free-living geniculate corallines (similar to rhodoliths for non-geniculate corallines) lacking a holdfast (Tâmega et al., 2017, 2021). They are a relatively new discovery and have so far been reported from Brazil (Tâmega et al., 2017, 2021), the west coast of Canada (Taylor & Saunders, 2025), and the French Mediterranean (Le Gall, unpub. data). In keeping with the growth forms for non-geniculate corallines (Maneveldt et al., 2026; Woelkerling et al., 1993), we have not made a distinction between attached and free-living specimens and have included articuliths in the respective growth forms outlined in the following rather than including them as

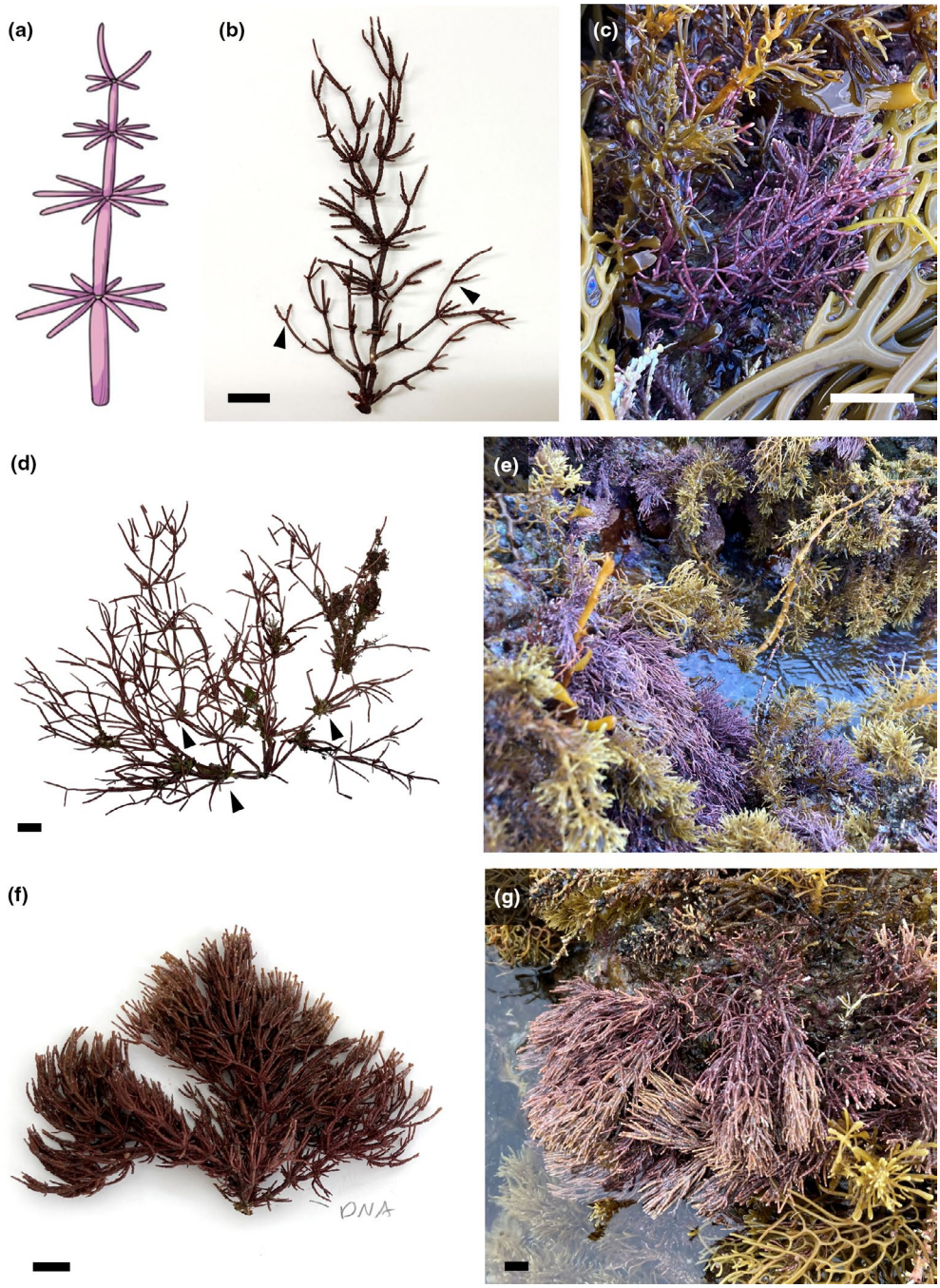

FIGURE 6 Examples of the *whorled* growth form. All scale bars = 1 cm. (a) Schematic drawing of the growth form. (b) *Metagoniolithon 'radiatum'* (JS91) with apparent verticillate (whorled) branching. Branching toward the ends dichotomous (arrow). Clear discoid (disc-like) holdfast. Devonport, Tasmania, Australia. (c) *Metagoniolithon 'radiatum'* (JS137) in the intertidal. Lighthouse Beach, Tasmania, Australia. (d) Large *Metagoniolithon 'radiatum'* with large clusters of branches in the middle of the plant (arrow). Lady Bay, Tasmania, Australia. (e) Numerous *Metagoniolithon* sp. individuals among *Cystophora* sp. near a tide pool. Couta Rocks, Tasmania, Australia. (f) Densely branched *Metagoniolithon 'radiatum'* with comparatively short intergenicula. Couta Rocks, Tasmania, Australia. (g) The same specimen in the low intertidal/shallow subtidal. Images: (b–g) Jakop Schwoerbel.

a separate growth form. When describing articuliths, we suggest combining the appropriate growth forms with the word articulith to illustrate the free-living nature of the specimen. The *Jania cabista* type specimen in Tâmega et al. (2021, fig. 18), for example, can be described as an *arbuscular* articulith. This approach also allows combinations with the non-geniculate growth forms from Maneveldt et al. (2026) when those may be more applicable: the apparent *fruticose* articuliths of *Calliarthron* that have dramatically reduced numbers of genicula (Taylor & Saunders, 2025, fig 1b/c), for example. Further research into articuliths may uncover more free-living geniculate coralline morphologies and may necessitate their inclusion as a separate growth form in

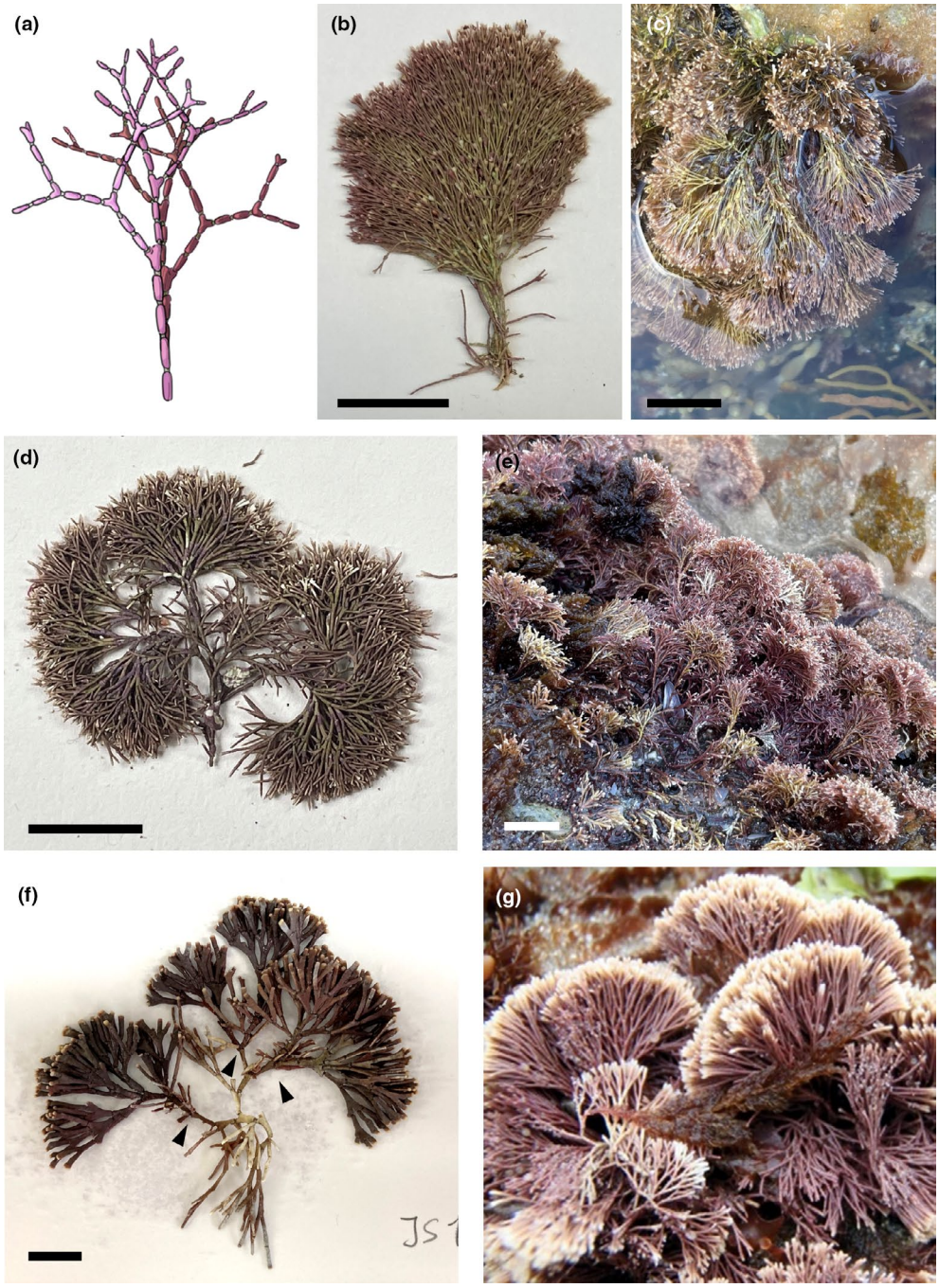

FIGURE 7 Examples of the *arbuscular* growth form. All scale bars = 1 cm. (a) Schematic drawing of the growth form. Different colors represent overlapping branching systems. (b) *Jania* sp. (JS145) with dense and fine overlapping *fan-like* branching. Lighthouse Beach, Tasmania, Australia. (c) The same specimen in the intertidal growing in dense tufts along the edge of a tide pool. (d) *Jania* sp. (PTM2202) with very dense, overlapping dichotomous branching. Tessellated Pavement, Tasmania, Australia. (e) The same specimen in the field forming dense clumps in the lower intertidal. (f) *Amphiroa 'anceps'* (JS100) with overlapping dichotomous and polychotomous branching and occasional true multiplanar branching (black arrowhead). George Rocks, Tasmania, Australia. (g) *Jania rubens*, Spain. Images: (b, c, f) Jakop Schwoerbel; (d and e) Patrick Martone; (g) Viviana Peña.

the future, but for now, there is not enough information on this group to warrant their separation.

It is important to stress that individuals may not necessarily fit neatly into any given growth form, as is often the case (Figure 9). To reflect this, the growth forms constitute the focal points of a network with intergrades between them that can accommodate "mixed growth forms" (Figure 10). These intergrades are often a consequence of different branching patterns in primary and higher-order branches. For example, most of the *Jania* specimens cited from Atlantic European coasts have dichotomous primary branches, with secondary branching

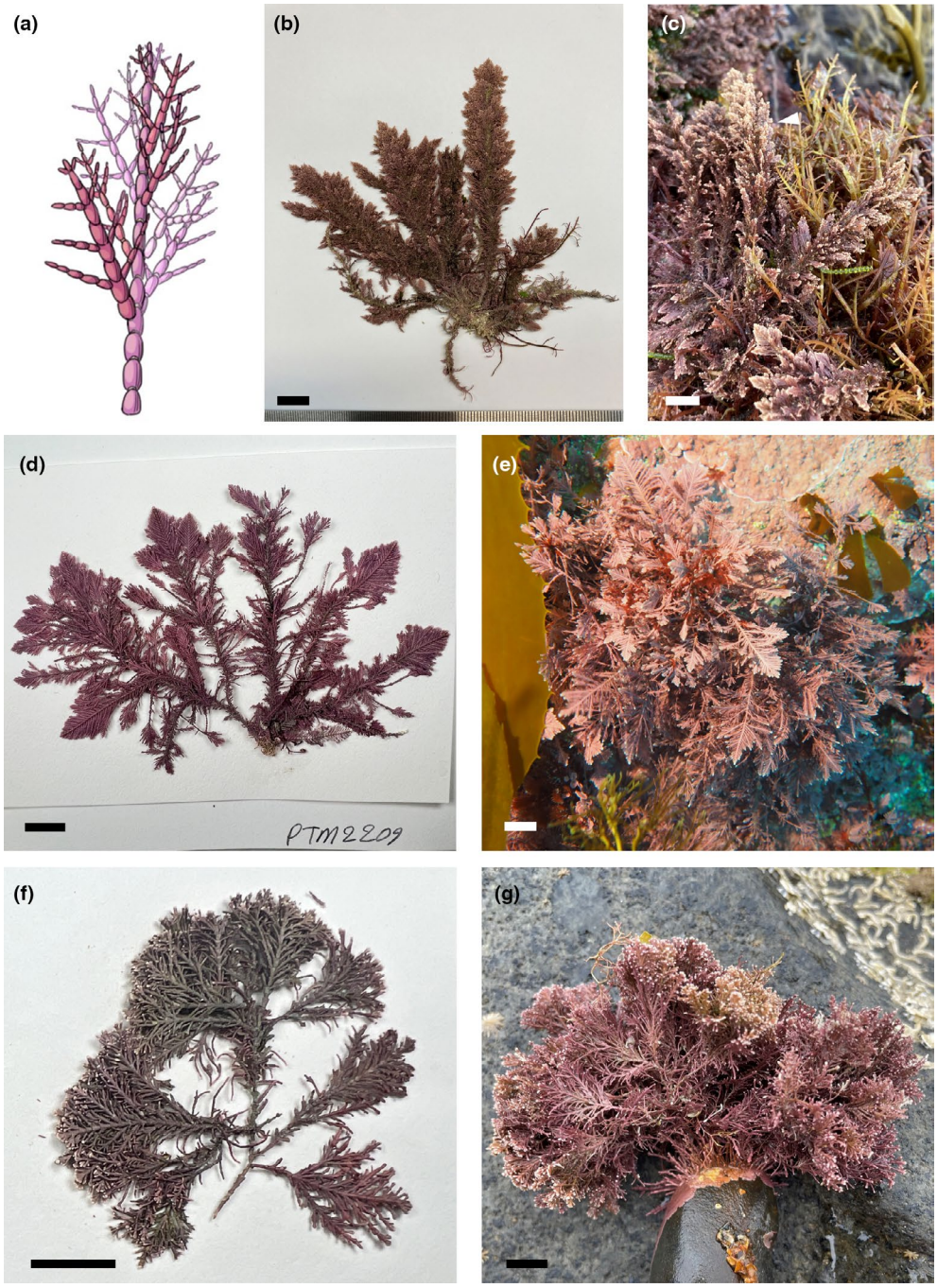

FIGURE 8 Examples of the *plumose* growth form. All scale bars = 1 cm. (a) Schematic drawing of the growth form. Different colors represent overlapping branching systems. (b) *Jania 'rosea'* (JS127) with dense overlapping pinnate (feathered) branches. Lighthouse Beach, Tasmania, Australia. (c) The same specimen in the field (white arrows). (d) *Jania 'rosea'* (PTM2209) with clear bipinnate branching. Sisters Bay, Tasmania, Australia. (e) A similar *Jania 'rosea'* specimen in the field. Twin Peaks, Tasmania, Australia. (f) *Corallina* sp. (PTM2268) with layered bipinnate branching. Stanley, Tasmania, Australia. (g) The same specimen in the field, growing on a pebble in the intertidal. Extensive crustose base visible with multiple erect axes. Images: (b, c) Jakop Schwoerbel; (d, f, g) Patrick Martone; (e) Hunter Forbes.

more variable—for example, pinnate (feathered), opposite, irregular, or dichotomous (Lugilde et al., 2017). Similarly, some *Jania* specimens in southern Australia have primary dichotomous branching, but pinnate "feathering" on higher-order branches (Figure 9a). Other specimens show a mix of characteristics from different growth forms without a clear separation between branch orders (Figure 9b,c). Similarly, *Amphiroa* '*fragilissima*' and *A.* '*gracilis*' individuals show, to varying degrees, a mix of dichotomous branching and polychotomous branch whorls (Harvey et al., 2013, *A.* '*fragilissima*', fig. 27A, C; *A.* '*gracilis*', fig. 30B).

Most species are not restricted to a single growth form, and individuals from the same species may

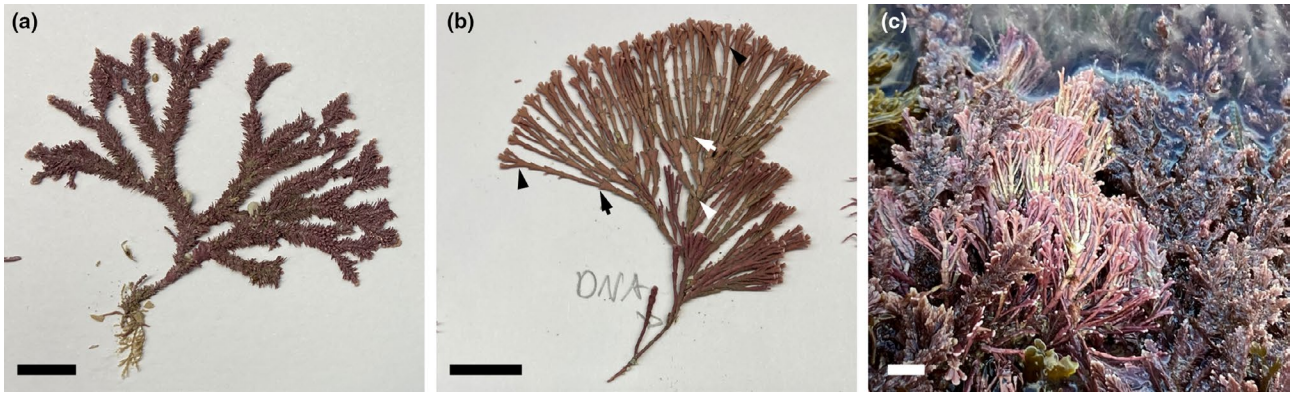

FIGURE 9 Examples of growth form intergrades. All scale bars = 1 cm. (a) *Jania* sp. (JS97) with dichotomously branched main axes and pinnate feathering. Ulverstone, Tasmania, Australia. (b) *Arthrocardia* sp. combining characteristics of several different growth forms including feathered (pinnate) branching (black arrowhead), dichotomous branching (black arrow) and polychotomous branching (white arrow). While most of the specimen is complanate a couple of branches are multiplanar (white arrowhead). Lighthouse Beach, Tasmania, Australia. (c) The same specimen in the intertidal zone. Images: (a–c) Jakop Schwoerbel.

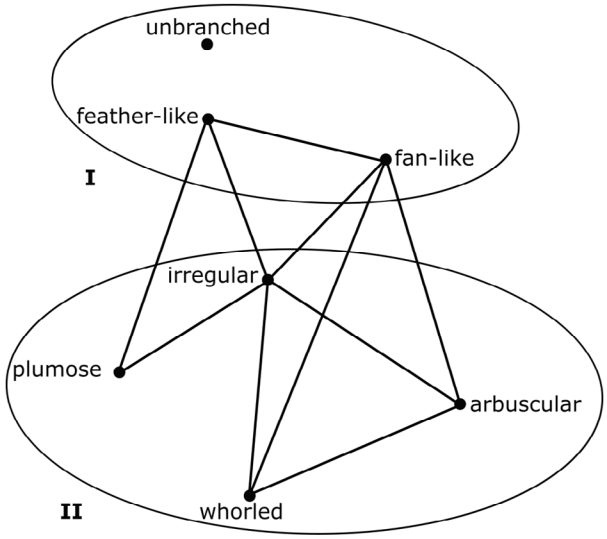

FIGURE 10 Growth form network with the seven focal points for geniculate coralline algae. Group I indicates two-dimensional growth forms and group II those with a three-dimensional appearance. Solid lines between focal points represent intergrades between growth forms.

display multiple growth forms as well as intergrades between these. These intergrades may depend on their environment or developmental stage, although this is difficult to confirm without DNA sequence data, given the unreliability of morphological and anatomical characters to identify species (Calderon et al., 2021; Lugilde et al., 2019). Twist et al. (2020) documented the importance of DNA sequencing to correctly identify all species of coralline algae due to the amount of cryptic diversity that has been revealed in studies conducted thus far. For geniculate corallines, the tribe Corallineae has provided some notable examples. *Corallina officinalis*, the generitype, in the Atlantic is *feather-like* (Brodie et al., 2013, fig. 1–2), whereas in the northeast Pacific, it is *irregular* and was regarded as a distinct genus, *Pachyarthron* (Woelkerling et al., 2008) prior to DNA sequencing (Hind et al., 2014). *Corallina berteroi* has growth forms ranging from *unbranched* to *feather-like* to *plumose* that reflect its cosmopolitan geographical distribution and what appear to be multiple evolving populations (Calderon et al., 2021). The growth form network can be used to define and illustrate a morphological "space" occupied by a species by combining different data types from multiple specimens: DNA sequencing (to determine species identity), morphological (the range of growth forms), and experimental/environmental data (potential drivers of these morphologies; Figure 11). Some of the observed morphological variation in coralline algae has been considered to be environmentally mediated; however, detailed studies investigating morphological variability in geniculate corallines, especially resulting from plastic responses to biotic or abiotic stressors, are scarce and are further complicated by cryptic diversity and often a lack of DNA sequences (Enríquez et al., 2009; Lugilde et al., 2019; Peña et al., 2020; Twist et al., 2020). Common-garden studies combining transplanting/translocation experiments with detailed morphological measurements and DNA sequencing are needed to understand the concept of plasticity in geniculate corallines and to better understand how these species are situated in the growth form network.

Unbranched individuals may have extensive crustose bases and only few upright axes. These uprights are often only a single intergeniculum in length (Figure 2b,c). The growth form is especially characteristic of species such as *Chiharaea americana* (Figure 2b; Martone et al., 2012, fig. 4). Rather than an intermediate between geniculate and non-geniculate corallines, these species represent geniculate corallines with a reduced number and size of uprights (Martone et al., 2012). As noted above, *Corallina*

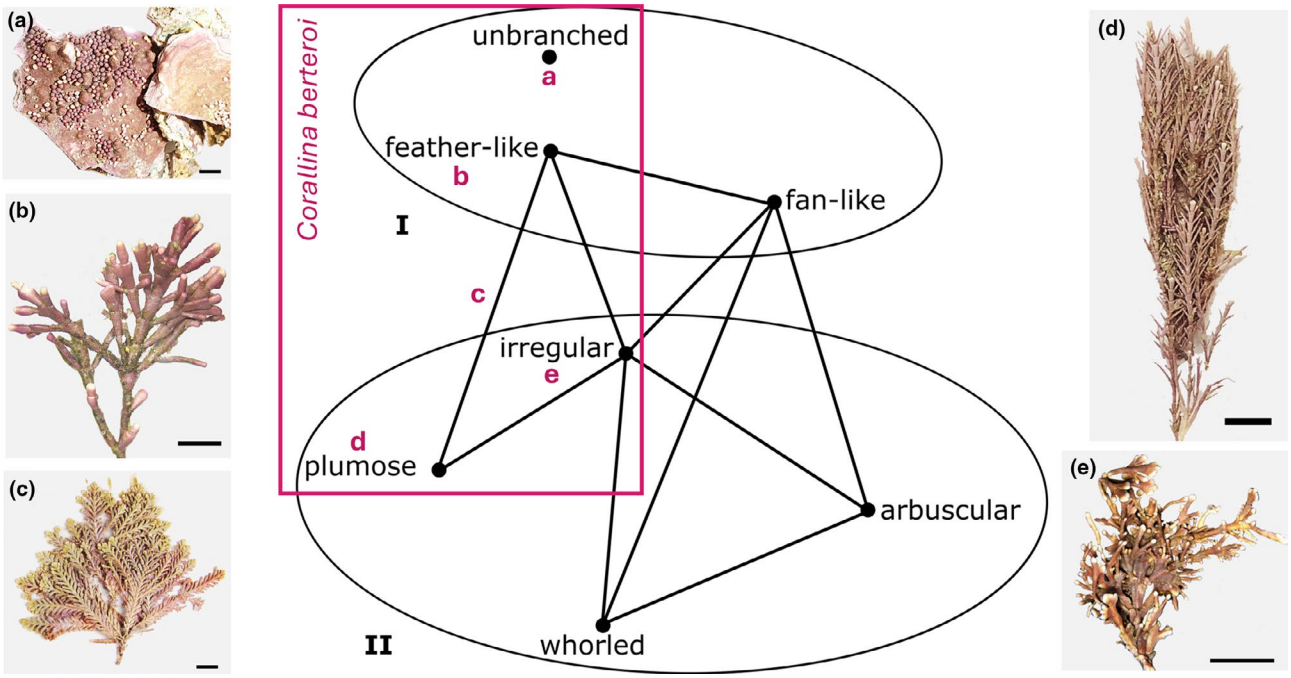

FIGURE 11 Illustration of the morphological space occupied by *Corallina berteroi* (pink box). Bold pink letters (a–e) show the position of specimens within the network. All illustrated specimens are adapted from Calderon et al. (2021) and have been confirmed by DNA sequencing. Growth forms were determined to place the shown specimens in the network, with the morphological space being defined as the range of growth forms occupied by all the studied specimens. If additional environmental or physiological data linked to the morphology are available, this could be used to identify drivers that push specimens in one direction or another within this morphological space. (a) *Unbranched* specimen, Chiba, Japan (UBC A62034), scale bar = 2 mm. (b) *Feather-like* specimen, Punta Arenas, Chile (LEMAS028), scale bar = 2 mm. (c) *Feather-like/plumose* specimen, California, U (UC 545769), scale bar = 5 mm. (d) *Plumose* specimen, North Carolina, United States (NCU 628550), scale bar = 5 mm. (e) *Irregular* specimen with a mix of pinnate (feathered) and polychotomous branching, Piura, Peru (CNU025339), scale bar = 5 mm.

berteroi is a morphologically variable species and, among other forms, also exists as unbranched thalli (Calderon et al., 2021, fig. 2). True unbranched geniculate corallines are relatively rare, but newly settled geniculate corallines, such as *Corallina* or *Bossiella*, often start as a crust with tiny, short uprights that can appear unbranched and minute like *Chiharaea* before they grow larger (Johansen, 1981). There are no known intergrades with other geniculate growth forms, but depending on the frequency of upright axes, *unbranched* individuals can appear similar to *encrusting* non-geniculate specimens (Maneveldt et al., 2026).

Complanate individuals comprise a major group of branched growth forms and include *feather-like* and *fan-like* growth forms. Both growth forms branch in one plane but are differentiated by their mode of branching and presence or absence of a percurrent (continuous central) main axis.

Feather-like individuals have pinnate (feathered) branching with a percurrent (continuous central) axis. Branch frequency varies from sparse (several intergenicula between branches, Figure 3b,c) to dense (branching at every intergeniculum, Figure 3e–g) and can be variable within individuals, for example, *Corallina yendoi* (Calderon et al., 2021, fig. 2). Branching can also appear sparse where the intergenicula are much longer than they are wide (Figure 3d). Some individuals form extensive crustose bases with many upright axes, which can make the differentiation between *feather-like* and *plumose* specimens difficult, and larger, older *feather-like* individuals often intergrade with the *plumose* growth form. *Feather-like* individuals can be observed in most geniculate coralline genera, such as *Corallina*, for example, *C. berteroi* (Pardo et al., 2015, figs. 20–21, as *C. caespitosa*), *C. parva* (Wade et al., 2023, fig. 7b), *C. vancouverensis* (Wade et al., 2023, fig. 6a) and *C. hombronii* (Brodie et al., 2021, fig. 4, as *C. chamberlainiae*). *Arthrocardia*, for example, *Ar. wardii* (Womersley & Johansen, 1988, fig 1A) and *Ar. 'carinata'* (Kogame et al., 2017, fig. 3a), and *Bossiella*, for example, *B. reptans* (Hind et al., 2015, fig. 12a), *B. frondescens* (Hind et al., 2015, fig. 8a), and *B. frondifera* (Hind et al., 2015, fig. 7a), are additional genera with many species exhibiting *feather-like* growth forms. *Jania 'rosea'* is, at present, the only species with this growth form in *Jania* (Harvey et al., 2020, figs. 20–25).

Fan-like specimens have dichotomous branching and lack a percurrent (continuous central) axis (Figure 4), differentiating them from the other complanate growth form (*feather-like*). Older and/or larger *fan-like* individuals regularly intergrade with the *arbuscular*

growth form. The *fan-like* growth form is widespread throughout geniculate coralline algal genera. Examples include *Arthrocardia* cf. *corymbosa* (Kogame et al., 2017, fig. 3b), *Amphiroa 'anceps'* and *A. 'crassa'* (Harvey et al., 2013, fig. 2B, 8A), *Calliarthron*, and some species of *Jania* (Harvey et al., 2020, figs. 27, 31).

Intergrades between the complanate growth forms are relatively common and can range from primary dichotomous branching with secondary pinnate (feathered) branching throughout, in species of *Jania* (Figure 9a; Lugilde et al., 2017, fig. 2K), for example, to more irregular branching (Lugilde et al., 2017, fig 2L). Separation of the complanate and multiplanar forms can be challenging in the field due to dense clusters of *fan-* or *feather-like* fronds appearing *arbuscular* or *plumose*, respectively. No free-living (articulith) complanate specimens have hitherto been reported.

Irregular individuals are easily identified based on their lack of a consistent branching pattern (Figure 5). This can include parts of an individual with distichous (opposite or alternate feathering), decussate (orthogonally stacked branches around a central axis), and/or dichotomous (with varying branching angles) branch arrangements. *Irregular* specimens are most often multiplanar but can be complanate. The *irregular* growth form may be the consequence of physical damage, wounding by grazing, or hydrodynamic forces, leading to unusually shaped intergenicula or missing branches. However, the impact of environmental drivers on geniculate coralline morphology is poorly understood at present (Enríquez et al., 2009; Lugilde et al., 2019). Specimens of *Calliarthron cheilosporioides* (Gabrielson et al., 2011, fig. 3), *Alatocladia modesta* (Gabrielson et al., 2011, figs 11–13), and *Corallina officinalis* in the northeast Pacific (Woelkerling et al., 2008, figs. 4, 23, 24, as *Pachyarthron cretaceum*) often show *irregular* branching. Due to the variety of different branching patterns shown by *irregular* individuals, this growth form has apparent intergrades with all other geniculate growth forms apart from *unbranched*.

Multiplanar individuals comprise the second major group of branched growth forms. Based on branching pattern, this group is divided into *whorled*, *plumose*, and *arbuscular* growth forms.

Whorled individuals are the only geniculate forms that exhibit a multiplanar branch arrangement with several branches originating at a single geniculum radially arranged around a percurrent (continuous central) axis (Figure 6). This arrangement results in a unique three-dimensional appearance (Figure 6c,g). This growth form is mainly known from the genus *Metagoniolithon* from southern Australia (Figure 6b–g; Ducker, 1979). With the exception of *M. 'chara* var. *dichotomum*,' branching in this genus is only initially dichotomous (Figure 6b), but their unique multitiered genicula remain meristematic and produce further branches, resulting in false whorls (Ducker, 1979). Similarly, whorled branchlets are also known from *Amphiroa* '*gracilis*' and *A*. '*fragilissima*' (Harvey et al., 2009, fig. 27A, C, fig. 46). Free-living, *whorled* articuliths have so far not been reported.

Arbuscular individuals form the multiplanar counterpart to the *fan-like* growth form. Branching is dichotomous or furcate (forking), sometimes with polychotomies, without a clear percurrent (continuous central) axis (Figure 7). Individuals branchlets are often *fan-like* and therefore complanate. The three-dimensional appearance is due to extensive overlapping secondary or even tertiary branching (Figure 7b–e). *Arbuscular* species can form dense mats in the intertidal zone, especially around the rims of tide pools. Close aggregations of *fan-like* individuals or fronds can be difficult to separate from *arbuscular* specimens at a glance, and intergrades are common. *Arbuscular* growth is most common in species of *Jania*, for example, *J. crassa* (Nelson et al., 2023, figs. 2–4), *J. sphaeroramosa* (Twist et al., 2018, fig. 3), and *J*. '*micrarthrodia'* (Harvey et al., 2020, fig. 6a), and in species of the genus *Amphiroa* such as *A. 'anceps'* (Figure 7f). Most hitherto documented articuliths are *arbuscular* with *Calliarthron* and *Bossiella* specimens having reduced genicula and an appearance resembling the *fruticose* growth form observed in non-geniculate corallines (Tâmega et al., 2017, 2021; Taylor & Saunders, 2025). Intergrades exist between *arbuscular* and *whorled* growth forms, as seen in *A. 'gracilis'* (Harvey et al., 2009, fig. 46).

Plumose fronds are the three-dimensional counterpart to the *feather-like* growth form. Even though each individual branch is often *feather-like* and thus complanate, extensive and overlapping secondary or even tertiary branching results in a three-dimensional appearance (Figure 8). Just as in *feather-like* individuals, branch frequency varies from sparse (several intergenicula between branches) to dense (branching at every intergeniculum) in *plumose* individuals and can be variable within the same specimen. Some species form extensive crustose bases with many upright axes that can make the differentiation between *feather-like* and *plumose* growth forms difficult. As with the dichotomous growth forms, larger and older *feather-like* individuals often intergrade with the *plumose* form. Frequently branching individuals often form dense tufts in the intertidal and subtidal zones (Figure 8b,g). *Plumose* specimens can generally be found in all genera that also show *feather-like* growth, notably some species of *Corallina* and *Bossiella*. Specific examples of often *plumose* species include *C. vancouverensis* (Wade et al., 2023, fig. 6c), *B. frondifera* (Hind et al., 2015, figs. 6a, b), *C. hombronii* (Brodie et al., 2021, fig. 5, as *C. chamberlainiae*) and *Jania 'rosea'* (Figure 8d,e). Free-living, *plumose* articuliths have so far not been reported.

In conclusion, like non-geniculate corallines, geniculate corallines can also be grouped into different growth forms. Here, the branching pattern is an integral part of the growth-form classification. The growth forms, and the network they form, provide standardized terminologies to describe the growth habits of coralline specimens and the morphological space occupied by coralline species. As a general resource to underpin the growth forms and to facilitate coralline taxonomy, we have provided a glossary of common terms related to these growth forms and intergenicular morphology. We hope that these tools will be a helpful resource for anyone interested in these fascinating and diverse macroalgae.

AUTHOR CONTRIBUTIONS

Jakop Schwoerbel: Conceptualization (lead); formal analysis (equal); methodology (equal); writing – original draft (lead); writing – review and editing (equal). **Juliet Brodie:** Conceptualization (equal); formal analysis (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Martha S. Calderon:** Conceptualization (equal); formal analysis (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Guillermo Diaz-Pulido:** Conceptualization (equal); formal analysis (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Paul W. Gabrielson:** Conceptualization (equal); formal analysis (equal); methodology (equal); writing – original draft (lead); writing – review and editing (equal). **Aki Kato:** Conceptualization (equal); formal analysis (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Line Le Gall:** Conceptualization (equal); formal analysis (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Gavin W. Maneveldt:** Conceptualization (equal); formal analysis (equal); methodology (equal); writing – original draft (lead); writing – review and editing (equal). **Clio Maridakis:** Conceptualization (equal); formal analysis (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Patrick T. Martone:** Conceptualization (equal); formal analysis (equal); methodology (equal); writing – original draft (lead); writing – review and editing (equal). **Isabella Moro:** Conceptualization (equal); formal analysis (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Robert J. Mrowicki:** Conceptualization (equal); formal analysis (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Wendy A. Nelson:** Conceptualization (equal); formal analysis (equal); methodology (equal); writing – original draft (lead); writing – review and editing (equal). **Viviana Peña:** Conceptualization (equal); funding acquisition (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Fabio Rindi:** Conceptualization (equal); formal analysis (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Florence Rousseau:** Conceptualization (equal); formal analysis (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Tom Schils:** Conceptualization (equal); formal analysis (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Frederico T. S. Tâmega:** Conceptualization (equal); formal analysis (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Riccardo Trentin:** Conceptualization (equal); formal analysis (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal).

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ORCID

Jakop Schwoerbel https://orcid.org/0000-0002-9354-7608
Juliet Brodie https://orcid.org/0000-0001-7622-2564
Martha S. Calderon https://orcid.org/0000-0003-3611-140X
Guillermo Diaz-Pulido https://orcid.org/0000-0002-0901-3727
Paul W. Gabrielson https://orcid.org/0000-0001-9416-1187
Aki Kato https://orcid.org/0000-0001-6124-9676
Line Le Gall https://orcid.org/0000-0001-7807-4569
Gavin W. Maneveldt https://orcid.org/0000-0002-5656-5348
Clio Maridakis https://orcid.org/0009-0007-3153-1073
Patrick T. Martone https://orcid.org/0000-0002-6345-1023
Isabella Moro https://orcid.org/0000-0002-7850-6031
Robert J. Mrowicki https://orcid.org/0000-0001-7767-9259
Wendy A. Nelson https://orcid.org/0000-0003-0014-5560

Viviana Peña https://orcid.org/0000-0001-7003-3850
Fabio Rindi https://orcid.org/0000-0002-7392-3653
Tom Schils https://orcid.org/0000-0002-1516-9082
Frederico T. S. Tâmega https://orcid.org/0000-0003-2773-2036
Riccardo Trentin https://orcid.org/0000-0002-2886-3364

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